

Identification and analysis of AP2/ERF gene family in tomato under abiotic stress

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Abstract: AP2/ERE-type transcription factors, as a type of plant-specific transcription factors, play a key role in plant biotic and abiotic stress. Meanwhile, they have been studied in many plants, but rarely in tomatoes. In this study, we performed a genome-wide analysis of the SLAP2/ERF gene family of tomato, and finally identified 29 SLAP2/ERF genes and divided them into different subfamilies. At the same time, its basic physical and chemical properties were analyzed. We also constructed phylogenetic trees with 30 *Arabidopsis* AP2/ERF proteins and 28 potatoes AP2/ERF proteins to ensure conservative homology between them. In addition, we mapped 29 SLAP2/ERF transcription factors on 10 different chromosomes; and identified 43 responsive plant hormones, responsive light signals, tissue-specific expression and stress response elements from 2000bp upstream of the promoter region, and we analyzed conserved motifs and gene structures of SLAP2/ERF. The tertiary structure of SLAP2/ERF protein was constructed by homology modeling, and the protein-protein interaction network was constructed based on *Arabidopsis* Thaliana. Finally, the expression pattern of tomato in different tissues was studied by using gene expression database, and the expression level of tomato under abiotic stress was detected by q-RT-PCR. These results provide comprehensive information for further study of the function of the SLAP2/ERF gene family.

Introduction

In most cases, plants are subjected to different biotic and abiotic stress, such as drought, salinity, and low temperature, which seriously affect their yield and quality. Therefore, during the long-term and continuous development, plants have evolved various defense mechanisms to resist various stresses, including carbohydrate accumulation, increased antioxidant enzyme activity, and induced resistance gene expression (Chinnusamy *et al.*, 2004; Hobert, 2008). Transcription factors are proteins that specifically interact with cis-regulatory element in the promoter region of eukaryotic genes and can activate or inhibit the transcription initiation of other genes, and it can regulate the gene expression by interacting with other transcription factors (Singh *et al.*, 2002). There are a lot of transcription factors in plants, which play an important role in the process of plant growth,

physiological and biochemical reaction, signal transduction and response to environment. Studies have shown that overexpression of transcription factor genes in response to stress can promote the expression of genes associated with stress resistance downstream and improve the stress resistance of genetically modified crops (Liu *et al.*, 1998; Gilmour *et al.*, 2000; Sakuma *et al.*, 2006). There are 5.9% of the total genes are transcriptional factors in *Arabidopsis* (Thamilarasan *et al.*, 2014).

Transcription factors are divided into AP2/ERF, WRKY, B-zip, NAC and MYB families according to their DNA binding domains (Thamilarasan *et al.*, 2014; Zhang *et al.*, 2010). AP2/ERE-like transcription factors are plant-specific transcription factors, which are characterized by at least one AP2 binding domain. The domain contains 60 to 70 amino acids and is highly conserved. Meanwhile, AP2/ERE transcription factors are involved in plant development and stress pathway (Guttererson *et al.* 2004; Licausi *et al.*, 2013). According to the AP2 domain, the AP2/ERE family is divided into three subfamilies. Among them, the AP2 subfamily contains two AP2 domains, the RAV subfamily

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includes one AP2 and one B3 domain, and the ERF subfamily contains one AP2 domain (Sakuma *et al.*, 2002). The first AP2/ERF gene, *APETALA2*, was found in *Arabidopsis thaliana*, and its function is mainly related to flower development (Jofuku *et al.*, 1994). The results show that AP2/ERF family is a plant-specific TF family, and its subfamily plays a key role in regulating plant growth and development, such as regulating flower, fruit development and leaf shape (Boutillier *et al.*, 2002; Aya *et al.*, 2014). RAV subfamily may be a negative regulator in plant growth and development, and it plays a key role biotic and abiotic stress in plant (Hu *et al.*, 2004; Sohn *et al.*, 2006; Licausi *et al.*, 2013). The ERF subfamily, which is mainly responsible for plant responses to environmental and biological stresses, plays a key role in plant resistance to stresses, and can activate the expression of stress-resistant genes, thus increasing plant resistance to stresses (Liu *et al.*, 2013). The TF gene of ERF-A1 group has been cloned from several plants, such as *Arabidopsis thaliana* (Novillo *et al.*, 2012), wheat (Soltész *et al.*, 2013) and Tea (Wu *et al.*, 2015). In addition, the role of these genes in enhancing cold resistance of plants has also been confirmed. In maize, Yeast one-hybrid test showed that *ZmERF1A* gene was involved in the expression of cold response genes (Hu *et al.*, 2004). Overexpression of *lsERF2a* increased the salt tolerance of genetically modified crops (Kudo *et al.*, 2014). ERF is mainly related to low temperature, disease resistance, hormones, and high salt (Singh *et al.*, 2002). AP2/ERF transcription factors have been shown to play a key role in flower development in *Arabidopsis* (Kunst *et al.*, 1989), some members of the AP2/ERF family are also link factors in various adversity signaling pathways (Liu *et al.*, 2013), and AP2/ERF genes have been identified in many plants, including *Arabidopsis* (Nakano *et al.*, 2006), Rice (Rashid *et al.*, 2012), Cauliflower (Li *et al.*, 2017), Cabbage (Song *et al.*, 2013), and Pear (Li *et al.*, 2018).

Tomato (*Solanum Lycopersicum*) is not only an important economic vegetable, but also an important model plant for studying plant pathogen interaction (Jiang *et al.*, 2019). In 2012, the world's annual tomato production exceeded 160 million tons, where China accounted for 50 million tons (<http://faostat.fao.org>). The tomato genome has been sequenced and assembled by the International Tomato Genome Sequencing Project (http://solgenomics.net/Organism/Solanum_Lycopersicum/genome). Simultaneously, tomato is economically important and is a model species for studying fruit maturation (Consortium, 2012). So, a high-quality genome sequence and more than 30,000 kinds of proteins have been obtained in tomato. In previous tomato AP2/ERF studies have shown that, over-expression of tomato *JERF1* in tobacco can improve salt tolerance and low temperature resistance (Wu *et al.*, 2007), and over-expression of tomato *JERF3* increases tolerance to drought, low temperature, high salt, and osmotic pressure. Overexpression of tomato *TERF2/LeERF2* in tomato and tobacco enhances tolerance to freezing damage (Zhang *et al.*, 2010), and overexpression of tomato *TSRF1* in rice can increase its tolerance to high osmotic pressure and drought (Quan *et al.*, 2010). Overexpression of tomato *SIERF3ARD* promotes the expression of PR genes such as *PR1*, *PR2*, and *PR5*, and

significantly increases resistance to bacterial wilt disease (Pan *et al.*, 2010). Li *et al.* (Li *et al.*, 2011) found that the overexpression of *AtCBF1* transgenic lines in tomato, through continuous expression of RAV transcription factors, ERF family genes, and disease-related genes (PR) significantly increased resistance to bacterial wilt. Further study showed that *SIERF5* could regulate the expression of *AtCBF1* and *PR* genes by regulating the expression of *SIRAV* gene, which leads to increased resistance to disease. Overexpression of tomato *Pti4* gene in *Arabidopsis thaliana* could improve the resistance to powdery mildew and bacterial spot disease (Venkatesh *et al.*, 2013). These studies suggest that AP2/ERF transcription factors play a key role in both biotic and abiotic processes.

However, tomato grown in northwest China is susceptible to various abiotic stresses such as drought and freezing, and its stress resistance is poor, while AP2/ERF transcription factors play a key role in plant response to adversity and it is also essential for the normal development of many plants and interacts with various proteins to regulate gene expression. By given the importance of the AP2/ERF family, therefore, this study is based on the database of tomato genome and transcriptome. Twenty-nine AP2/ERF transcription factors were identified and systematically analyzed in tomato by bioinformatics, including the conserved domains and motifs, phylogeny, basic physical and chemical properties, gene structure, promoters and their expression in different tissues. At the same time, the expression pattern of AP2/ERF gene under abiotic stress was studied, which laid a solid foundation for the application of AP2/ERF transcription factor in genetic improvement of tomato.

Materials and Methods

Plant materials and treatments

Identification of AP2/ERF transcription factor family genes in tomato

Tomato genome data from the Phytome (Version 12.1) database (<https://phytozome.jgi.doe.gov/pz/portal.html>) was downloaded. Also downloaded the Hidden Markov model file (PF00847) (Finn *et al.*, 2008) of AP2/ERF transcription factor in the Pfam database (<http://pfam.xfam.org/>). Using Hmmer 3.0 software based on hidden Markov Model (HMMs), the AP2/ERF gene family of tomato was searched and identified by $e \leq 0.01$. The identified genes were submitted to Pfam (<http://pfam.xfam.org/family>), NCBI-CDD (<https://www.ncbi.nlm.nih.gov/cdd/>) and SMART (<http://smart.embl-heidelberg.de/>) online tools to predict the conserved domain of AP2/ERF protein, recorded the location of the conserved domain, and to eliminate the false-positive gene sequences (Letunic *et al.*, 2015).

Analysis of physical and chemical properties of Tomato AP2/ERF family

The Amino acid number, isoelectric point, molecular weight and hydrophobicity of 29 tomato AP2/ERF candidate proteins were analyzed in Expasy (<https://web.expasy.org/protparam/>).

Evolutionary analysis of AP2/ERF transcription factor family in tomato

28 AP2/ERF transcription factors of potato and 30 AP2/ERF transcription factors in *Arabidopsis* were identified from the Phytomaze database. Using the Clustal W function in MEGAX software, we compared the conserved amino acid sequences of identified AP2/ERF family proteins in tomato, *Arabidopsis thaliana*, and potato. The results were used to construct the phylogenetic tree using the proximity method and the Poisson model, the number of repetitions is 1000 (Song *et al.*, 2014) and the other parameters were set to default. The tree of evolution is beautified through the online software named Evolview (<http://120.202.110.254:8280/evolview>).

Structure analysis and chromosomal location of AP2/ERF transcription factor gene in tomato

The Gene Structure Display Server GSDS tool (<http://gsds.cbi.pku.edu.cn/>) (Hu *et al.*, 2015) was used to identify exon and intron structure of the gene. The conserved amino acid motifs were analyzed (Bailey *et al.*, 2006) by using MEME online software (<http://meme-suite.org/tools/meme>). The number of motif searches was set to 10, and other parameters were default. According to AP2/ERF gene's position in the tomato genome, 29 AP2/ERF genes were located on corresponding chromosomes by Mapchart software (Voorrips, 2002).

Promoter analysis, homology modeling and protein interaction network mapping of tomato AP2/ERF family genes

The upstream 2000 bp sequence of the SLAP2/ERF family gene was extracted from the tomato genome database as a promoter region, and the gene cis-regulatory element was analyzed by Plantcare online software (Lescot *et al.*, 2002). The SLAP2/ERF protein's three-level structure was modeled by Swiss-model server (Kelley *et al.*, 2015). We used String (<http://stringdb.org/>) online software (Franceschini *et al.*, 2013), based on *Arabidopsis*, to predict protein-protein interaction networks based on tomato and *Arabidopsis* homologous genes.

Analysis of the gene ontology (GO)

The function of SLAP2/ERF family in tomato was annotated by using Blast2GO program (Ye *et al.*, 2006) (<http://www>.

geneontology.org/) with default setting apart from e-value: 1.0×10^{-3} .

Gene expression analysis

Database of tomato gene expression (Tomato Functional Genomics Database) was used to search the expression data of SLAP2/ERF gene in different tissues. FPKM (Fragments Per Kilobase of transcript per Million Fragments mapped) as an indicator of gene expression level. Heat maps were created by using TBtools.

The total RNA of each sample (Tomato Leaf of different treatments, including 20% PEG, 100 mmol/L NaCl, 100 μ mol/L ABA, 100 μ mol/L SA, 4°C low temperature) was extracted with Rneasy small plant reagent box (Qiagen), and the cDNA was prepared with Superscript[™] III reverse transcriptase reagent box (Invitrogen). Real-time fluorescent quantitative pcr primers are shown in the following Tab. 1 and have been synthesized commercially. qRT-PCR analysis was performed in abi-viia 7 real-time PCR systems of American applied biosystems by 2 quantities ect-sybr-green-pcr-mix (Qiagen). Tomato actin (Action) gene was used as endogenous control. The relative gene expression level was calculated by $2^{-\Delta\Delta Ct}$ (Livak and Schmittgen, 2001). Each experiment was repeated three times with a separate RNA sample.

Results

Identification of AP2/ERF gene family members and analysis of physicochemical properties

The database of tomato proteins was searched by HMMM 3.0 software, and the conserved domains were identified by PFAM, SMART and NCBI-CDD. A total of 29 genes with typical AP2 domains were identified (Fig. 1). The analysis of the basic physical and chemical properties of AP2/ERF gene family (Tab. 2) showed that the number of amino acids were 120–677, the relative molecular weight was 13755.10–75240.22, there were 14 basic proteins (PI > 7) and 15 acidic proteins (PI < 7). An interesting phenomenon is that the hydrophobic index of all proteins in this family is less than 0, and they are all hydrophilic proteins.

TABLE 1

Primer information of 10 SLAP2/ERF genes by qRT-PCR

Gene name	Forward primer	Reverse primer
SIAP2-02	TGGACCAAGCTATAACACGCCATC	AAGCAGAAGCCGAAGCAGAAGAAG
SIAP2-05	GTTCGGAAGAGGAAACGAGGTGAG	TGTGGCGGGCAGTAGAAAATTCG
SIAP2-07	AACGGAGACACTTGCAACACG	GTCCACGGCGGCTCTTCTTAATAG
SIAP2-08	GAGGAGGTATGGCTCACAGTTTGC	TGTTGCTGCTGCTGATGTCTAGTG
SIAP2-09	AGAGGGGTAAGAAGGAGGCCATG	AAGCCGCCTTGTCATAAGCCATAG
SIAP2-14	ACAACCAGCAGCAGCAGATGAC	GATAGCAGAGACGGGTGGCATTG
SIAP2-15	GAAGGAGGCCATGGGGTAAATA	CAATGCAGCTTCTTCAGCAGTGTC
SIAP2-22	GGAGAGAAGCGGTGGAAACTGAAG	TGACGGCGTTAATGGACATGACTC
SIAP2-24	CTTACGATGCCGCTGCCAGAG	TCCACGGTACTGCTCCCACAC
SIAP2-26	ATCGGAACCGCCACTTGTCATG	ATTCCCACCGGCCAGTCCTC

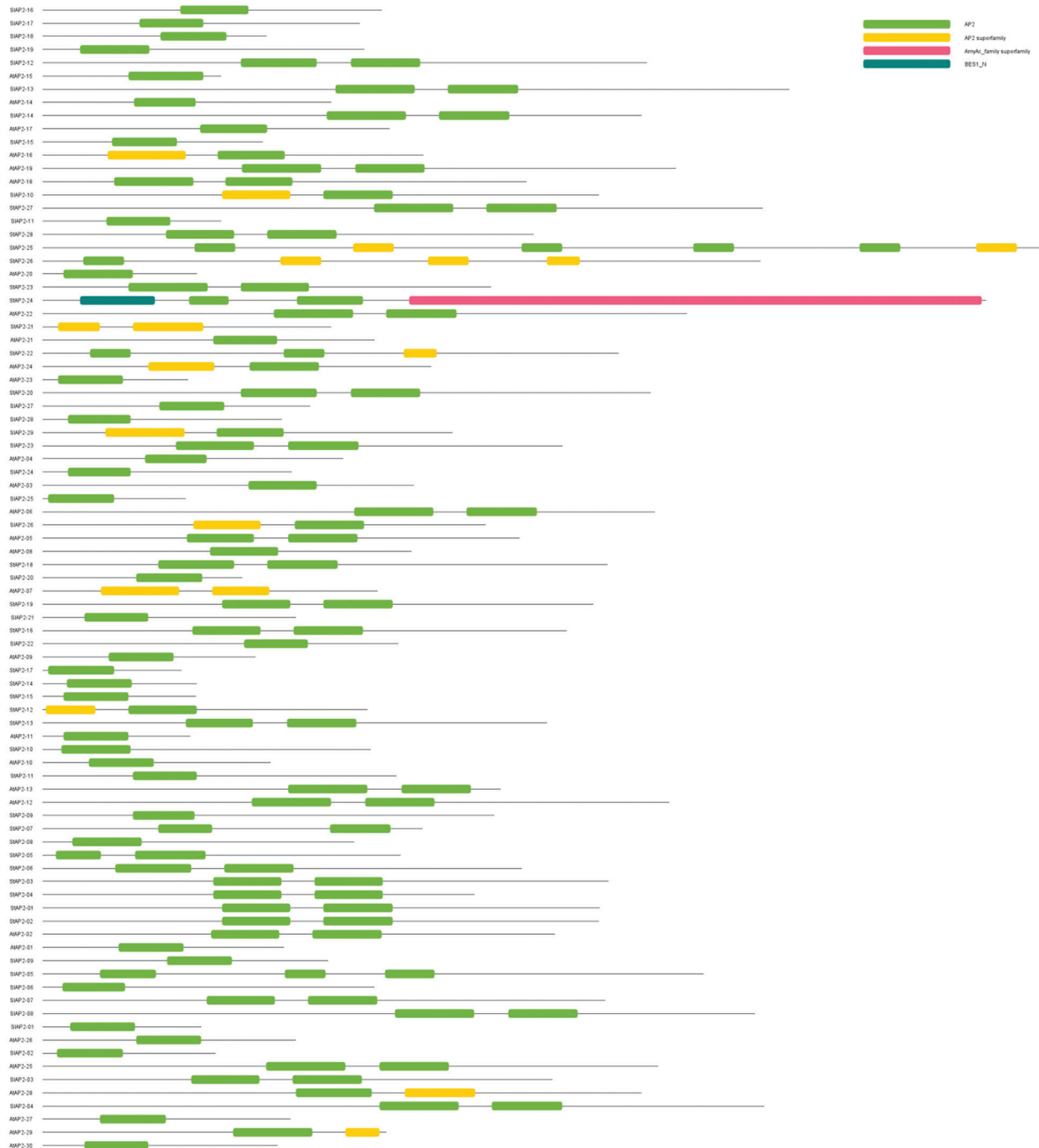


FIGURE 1. AP2 conserved domain of SLAP2/ERF proteins in tomato.

Phylogenetic analysis of members of AP2/ERF gene family

In order to study the phylogenetic relationship of tomato, we constructed a phylogenetic tree of 87 AP2/ERF transcription factors amino acid sequences of tomato, potato and *Arabidopsis thaliana* by using MEGA software based on the ClustalW multiple sequences (Supplementary File Tab. S1). A total of 8 branches were identified in the phylogenetic tree (Fig. 2), each group containing a different percentage of gene members. In the first group, there were only 3 SLAP2/ERFs and 4 StAP2/ERFs; in the second group, 9 SLAP2/ERFs, 3 StAP2/ERFs and 4 AtAP2/ERFs; in the third group, 1 SLAP2/ERF and 4 AtAP2/ERFs; in the fourth group, 1 SLAP2/ERF, 3 StAP2/ERFs and 7 AtAP2/ERFs; and in the fifth group, 2 SLAP2/ERFs and 2 StAP2/ERFs; group 6 has 1

StAP2/ERF and 1 AtAP2/ERF; group 7 has 4 SLAP2/ERFs, 8 StAP2/ERFs and 3 AtAP2/ERFs; and group 8 has 7 SLAP2/ERFs, 8 StAP2/ERFs and 11 AtAP2/ERFs. The phylogenetic tree showed that there were intraspecific and intraspecific homology between tomato, *Arabidopsis*, and potato. Five pairs of orthologous homologous genes between *Arabidopsis* and tomato, and 10 pairs of orthologous homologous genes between tomato and potato. There were 5 pairs of paralogous homologous genes between *Arabidopsis thaliana* and potato. There were 2 pairs of paralogous homologous gene pairs in tomato, 5 pairs of paralogous homologous gene pairs in potato and 5 pairs of paralogous homologous gene pairs in *Arabidopsis*. Meanwhile, the results showed that all the genes in the seventh and eighth branches contained two

TABLE 2

Basic characteristics of tomato (AP2) genes

Phytozome gene ID	Gene name	Protein length (aa)	Molecular weight (Da)	pI	GRAVY	Chr.position
Solyc09g089910.1.1	SLAP2-01	143	16158.76	5.77	-0.891	Chr09:699945342-6999495
Solyc09g066350.1.1	SLAP2-02	156	17764.37	7.08	-1.104	Chr09:65014582 -65015052
Solyc10g084340.2.1	SLAP2-03	462	51081.25	6.06	-0.677	Chr10:64051146-64055505
Solyc04g077490.3.1	SLAP2-04	654	71838.75	7.16	-0.646	Chr04:62512499 -62519587
Solyc04g009450.1.1	SLAP2-05	599	67226.97	9.11	-0.790	Chr04: 2859935 -2861734
Solyc02g067020.1.1	SLAP2-06	300	34110.17	5.60	-0.692	Chr02:37828480-37829382
Solyc02g093150.3.1	SLAP2-07	510	56999.91	6.69	-0.803	Chr02:54715052 -54718090
Solyc02g092050.3.1	SLAP2-08	646	72002.33	6.62	-0.806	Chr02:53895704 -53902352
Solyc02g077360.1.1	SLAP2-09	258	30015.52	4.96	-0.791	Chr02:42885146 -42885922
Solyc02g064960.3.1	SLAP2-10	504	57299.16	8.51	-1.018	Chr02:36641329 -36645265
Solyc02g077370.1.1	SLAP2-11	161	18051.27	7.69	-0.526	Chr02:42890880 -42891365
Solyc11g061750.2.1	SLAP2-12	548	60739.39	6.10	-0.816	Chr11:48672010-48678655
Solyc11g008560.2.1	SLAP2-13	677	75240.22	6.27	-0.818-	Chr11:2752880- 2752962
Solyc11g010710.2.1	SLAP2-14	543	59744.62	6.13	-0.628	Chr11:3760004- 3760583
Solyc11g006050.1.1	SLAP2-15	199	22541.83	4.83	-0.729	Chr11: 854696 -855295
Solyc12g056980.1.1	SLAP2-16	307	33663.72	8.65	-0.539	Chr12:64012226 -64013239
Solyc12g042210.2.1	SLAP2-17	287	33337.47	6.90	-1.108	Chr12:58194225-58194544
Solyc01g090300.2.1	SLAP2-18	202	22735.46	7.80	-0.651	Chr12:58194225-83839843
Solyc01g091760.2.1	SLAP2-19	291	32393.42	7.10	-0.801	Chr01:83839127 -85217581
Solyc01g090310.2.1	SLAP2-20	180	20417.70	7.88	-0.818	Chr01:83847469-83848168
Solyc08g007830.1.1	SLAP2-21	299	26020.79	4.99	-0.767	Chr08:2339145 -2339834
Solyc08g078190.1.1	SLAP2-22	322	36263.72	6.10	-0.565	Chr08:62147117 -62148085
Solyc07g018290.3.1	SLAP2-23	471	52749.14	8.34	-0.806	Chr07:10014430 -10019198
Solyc07g053740.1.1	SLAP2-24	225	24087.23	9.30	-0.434	Chr07:62294729 -62295406
Solyc03g005500.1.1	SLAP2-25	120	13755.10	6.07	-0.893	Chr03: 383587 -383976
Solyc03g044300.3.1	SLAP2-26	401	44944.48	7.68	-0.864	Chr03:8790516 -8795225
Solyc03g093610.1.1	SLAP2-27	242	26760.38	7.68	-0.433	Chr03:56458291 -56459019
Solyc03g006320.1.1	SLAP2-28	216	22442.29	9.04	-0.303	Chr03: 924296 -924946
Solyc03g117720.3.1	SLAP2-29	371	42093.77	6.77	-0.893	Chr03:68259122 -68263665

Note: GRAVY represents grand average of hydropathicity.

typical AP2 domains, belonging to the AP2 subfamily. All the genes in the second branch to the sixth branch contained an AP2 domain, belonging to a typical ERF subfamily. The SLAP2-05, StAP2-22, StAP2-25, and StAP2-26 genes in the first branch all contain more than 2 AP2 domains.

Gene structure analysis and chromosome localization of tomato AP2/ERF transcription factor

Since the global pattern of intron positions in some gene families served for the evolution of typical mark (Del Campo *et al.* 2013; Rogozin *et al.*, 2005), and the absence of introns could lead to the diversity of genetic structure, so we investigated SLAP2/ERF family introns-explicit substructure, to further study the evolution of their relationship. The results (Fig. 3B) showed that all 16 genes of class I and III of the SLAP2/ERF family have not contain intron structure, the 11 genes in the II groups all contain

introns, and the number is between 7 to 9, and the main gene structure is 9 exons and 8 introns (8 of 11 SLAP2s). In order to further study the structural diversity of tomato AP2/ERF protein, ten conservative motifs were revealed by Meme (Fig. 3C). We can conclude that AP2/ERF proteins clustered in the same group have similar motif domains (Fig. 3A), and all 29 genes contain motif1 and motif2, in which motif1 mainly contains the conserved domain L3-G5-A12 (Leu3-Gly5-Ala12) and motif2 contains a highly conserved domain Y1-R2-G3 (Tyr1-Arg2-Gly3). A gene with an AP2 domain, it can be divided into ERF subfamily and DERB subfamily according to the amino acid category of 14 and 19 (14 is valine, 19 is glutamate belongs to DERB subfamily, 14 is alanine, 19 is L-aspartic acid belongs to ERF subfamily). The genes in class I all belong to ERF subfamily and contain a typical AP2 domain, the genes in Class II all belong to AP2 subfamily and contain two typical

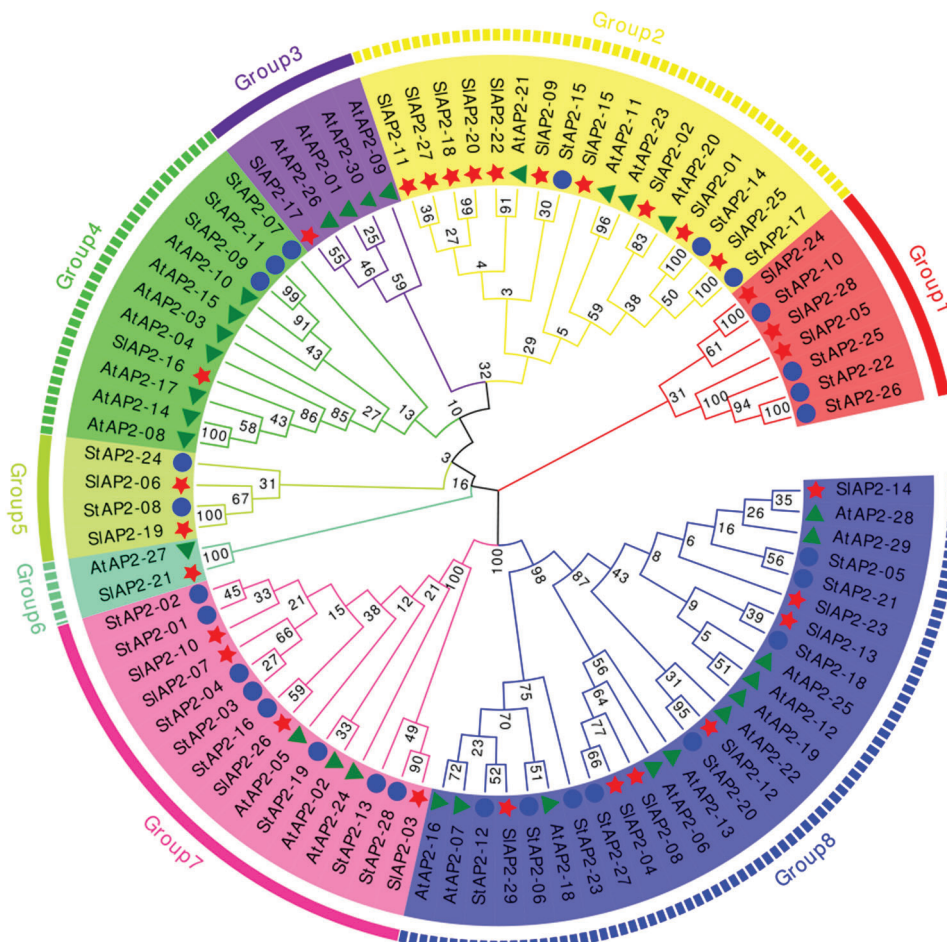


FIGURE 2. Phylogenetic analysis of AP2/ERF transcription factors from tomato and other plants. The phylogenetic tree was constructed using 30, 28, and 29 AP2/ERF protein sequences from *Arabidopsis*, tomato, and potato, respectively. AP2/ERF members were divided into eight clades.

AP2 domains, and the genes in Class III contain an AP2 domain, but the 14 and 19 loci of the domain are both valine and L-aspartic acid, so they are both ERF subfamily and DERB subfamily.

The physical genome annotation files were obtained from genome sequences in phytozome database, and the 29 SIAP2/ERF genes identified were located on 10 chromosomes (Fig. 4). In general, SIAP2/ERF gene was distributed unevenly on the chromosomes. The highest chromosome 2 (6 genes) and the lowest chromosome 10 (1 gene), it suggests that the AP2/ERF gene family may have multiple functions in tomatoes. Meanwhile, it can be concluded that the genes clustered in the same subgroup in the phylogenetic tree are basically on the same chromosome.

Promoter analysis of AP2/ERF gene in tomato

In order to study homeopathic components of the promoter region of SIAP2/ERF genes, we intercepted the 2000 bp sequence upstream of transcription initiation for analysis by Plantcare online software. A total of 43 homeostatic components related to tissue-specific expression, plant hormone response, light response and stress response were screened (Fig. 5). We found that all SIAP2/ERF family genes contain multiple TATA box homeopathic response elements; secondly, there are many types of light-responsive elements, and they exist in 26 SIAP2/ERF gene families (except SIAP2-11, SIAP2-25 and SIAP2-28); in plant hormone response elements, CGTCA-motif and TGACG-

motif are present in almost every gene; and we can also observe that some homeopathic elements are only present in a certain gene (SIAP2-15 in WUN-motif, TGA-box is in SIAP2-19, RY-element is in SIAP2-05, AT-rich element is in SIAP2-15, HD-Zip 1 is only in SIAP2-05). These results indicate that different SIAP2 genes regulate plant growth and development by responding to different homeopathic elements.

Analysis of homology model and construction of protein-protein interaction network

The Swiss-model online software was used to 3D model of the SIAP2/ERF protein family members (Fig. 6). The prediction model was based on the reported template, which was based on the maximum sequence fragment coverage, sequence identity, and credibility score of the test sequence. In addition, in order to clarify the similarity or difference of the generated models, the overlay structure is used to calculate the structural coverage. Structural coverage between the SIAP2 protein and the corresponding model sequence is more than 60%, indicating that the structural prediction of the SIAP2/ERF protein is relatively reliable. The three-dimensional model results show that these SIAP2/ERF proteins have similar tertiary structures, which mean that the SIAP2/ERF proteins may have evolved from the same ancestral sequence, or remained stable during long-term domestication after initial differentiation under the effect of purification selection.

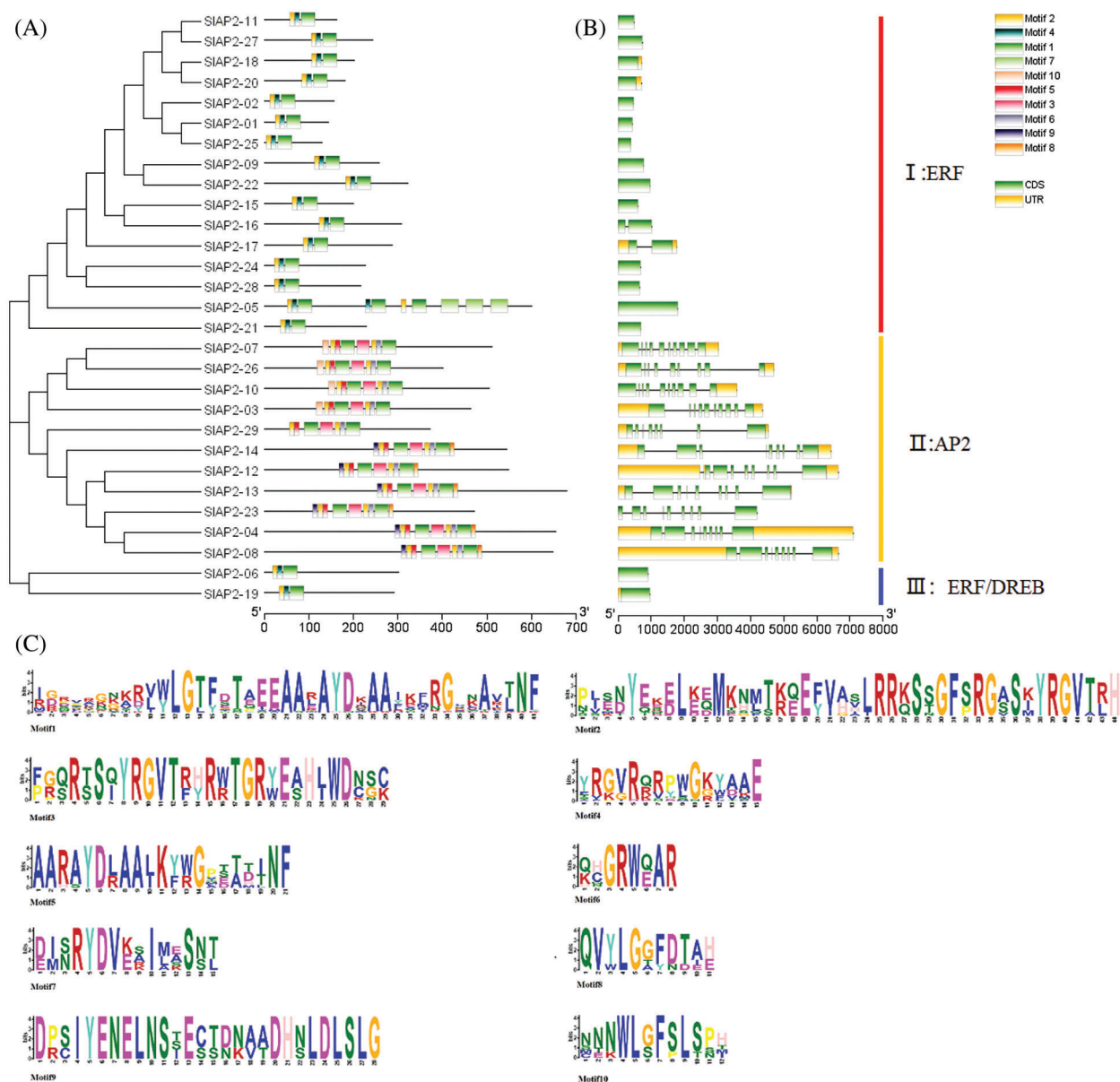


FIGURE 3. Gene structure and conserved protein domains of AP2/ERF.

A: The motif of AP2/ERF proteins. B: The intron-exon structures of SIAP2/ERF genes, including exons, introns. C: 10 conserved motifs sequence. Conserved motifs (1–10) are represented by different colored boxes while nonconserved sequences are shown by gray lines.

To further understand the function of SIAP2/ERF genes, we used String (<http://STRING.db.org/>) to predict the protein-protein Interaction network of the SIAP2/ERF gene family in tomato and *Arabidopsis*. The results showed (Fig. 7) that all the SIAP2/ERF proteins appeared in the known interaction network of AP2 proteins in *Arabidopsis*, which indicated that there was a close relationship between *Arabidopsis* and tomato. The results also showed that the protein structure and sequence of *AtRAP2.11* were similar to those of two SIAP2/ERF proteins (SIAP2-06, SIAP2-19), and its function may be involved in regulation of gene expression through stress factors and components of the stress signal transduction pathway. *AtERF1* is similar to three SIAP2/ERF proteins (SIAP2-11, SIAP2-15, and SIAP2-27). It may act as a transcriptional activator, bind to the promoter elements related to GCC-box, participate in the regulation of gene

expression during plant development, and be mediated by stress factors and components of stress signal transduction pathway. Similarly, *AtERF4* is structurally similar to SIAP2-24 and SIAP2-28, acting as a negative regulator of JA response to gene expression and fusarium oxysporum resistance to necrotizing fungal pathogens, and antagonizing TA inhibition of root elongation. *AtANT* is also involved in the initiation and development of organs, including floral organs, which maintain the cell's ability to be divided.

Gene ontology

SIAP2/ERF genes were annotated with Blast2GO. Among them, 17 genes were annotated in the GO database. According to the Fig. 8, SIAP2/ERF genes can be divided into three groups: biological process, molecular function, and cellular component. There were 17 genes (58.62%)

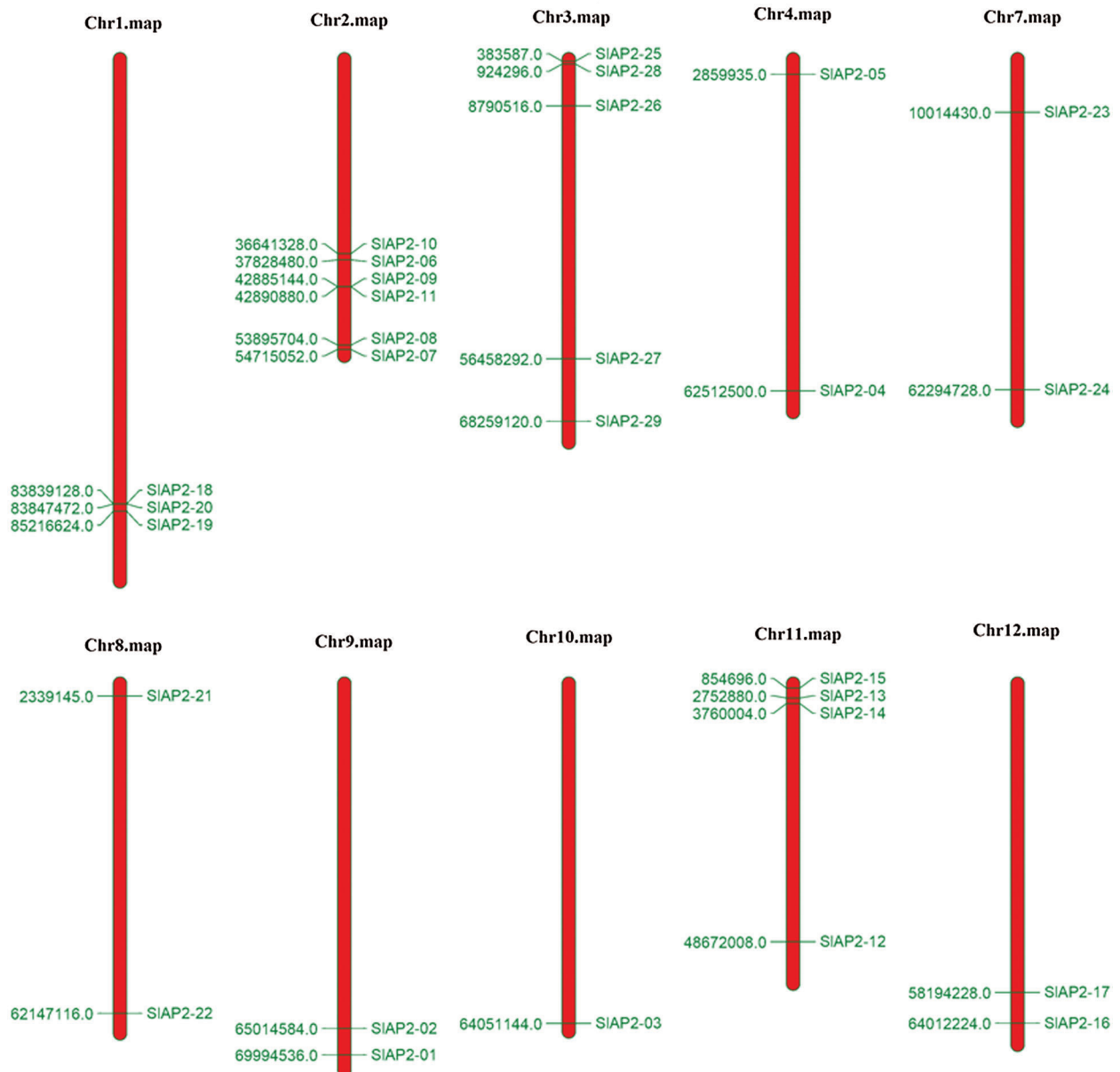


FIGURE 4. Distribution of SIAP2/ERF genes in chromosomes and the location of SIAP2/ERF transcription factors.

belonging to the biological process. Which transcription, DNA-templated (GO: 0006351) accounted for 16 genes (55.17%), followed by defense response (GO: 0006952) and ethylene-activated signaling pathway (GO: 0009873). In terms of molecular function, 13 SIAP2/ERF family genes are responsible for only two functions, DNA binding (GO: 0003677) and transcription factor activity (GO: 0003700). All 13 members of this family (44.82%) reside in the nucleus (GO: 0005634) and no other type sites exist in cellular component. We were able to observe an interesting phenomenon, where some SIAP2/ERF genes are involved in multiple biological processes, exist in the same cell component, and have multiple biological functions. These results suggest that the family genes are quite significant in nuclear development. For example, SIAP2-27 is located in the nucleus and has transcription factor activity and DNA binding, and it plays a key role in resistance to adversity, fruit ripening and activation of signaling pathways.

AP2/ERF gene expression profile analysis and expression analysis under biotic and abiotic stress by qRT-PCR

In order to analyze the expression profile of the AP2/ERF gene, we searched the tomato expression database for AP2/ERF gene expression abundance patterns in multiple tissues and organs (including flower, fruit on day 10 after flowering, fruit on day 20 after flowering, mature fruit, cotyledons, hypocotyls, meristems, mature leaves, roots, flower buds and young leaves). Heat map results (Fig. 9) showed that most of the genes have tissue expression specificity. For example, the SIAP2-03 gene is only highly expressed in the fruit on the 10th day after flowering, and SIAP2-26 is only specifically and highly expressed in mature fruit. It was observed that SIAP2-14 and SIAP2-16 were highly expressed in multiple tissues.

SIAP2/ERF transcription factors play a key role in abiotic stress, in order to further study the functions of these factors. We selected some specific genes through expression profile data in different tissues and homeopathic elements in the

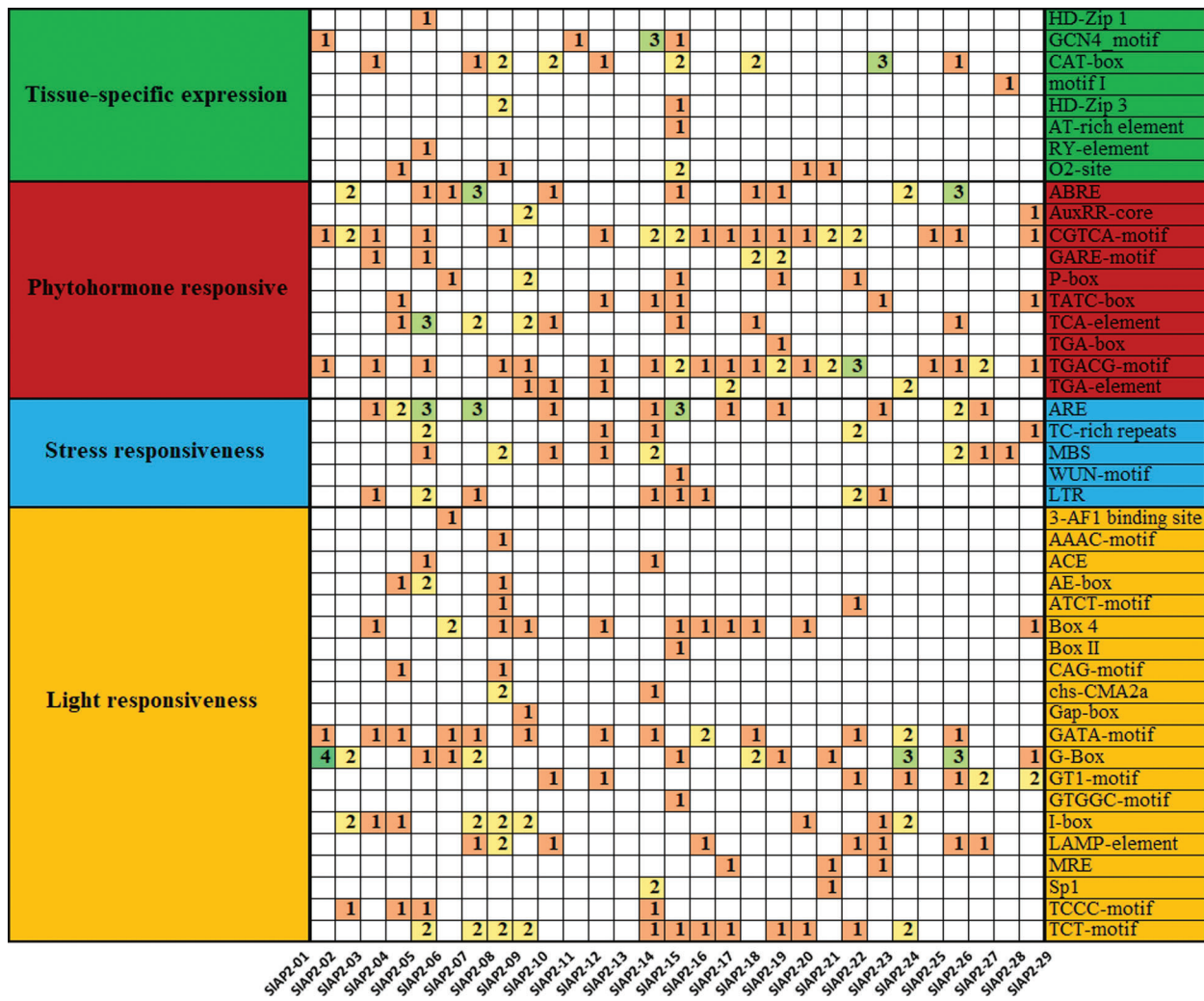


FIGURE 5. Analysis of cis-elements in promoters of 29 SLAP2/ERF genes. The 2000 bp promoter regions (upstream DNA sequence of the 5'-UTR) of each SLAP2/ERF gene were analyzed for cis-elements. Different cis-elements were indicated by different colored diagrams.

promoter region. Under abiotic stress (20% PEG, 100 mmol/L NaCl, 100 umol/L ABA, 100 umol/L SA, 4°C low temperature), we studied the transcriptional abundance of these genes in tomato seedling leaves. The results showed that basically all 10 SLAP2/ERF genes responded to these abiotic stresses (Fig. 10). Among them, the expression of SLAP2-02 and SLAP2-22 changed significantly after NaCl treatment for 2 h and 4 h, and after low temperature treatment for 8 h and 12 h, while the expression levels were very low under other abiotic treatments. It is also interesting to observe that the expression pattern of most genes under five different treatments in the form of first increase and then decrease. When most of genes (SLAP2-05, SLAP2-07, SLAP2-08, SLAP2-09, SLAP2-14, SLAP2-15, SLAP2-24, and SLAP2-26) were treated for 8 h, the expression of the genes in the 5 treatments was significantly higher than that in the control. Meanwhile, under the NaCl treatment, we can clearly observe the expression pattern of some genes which increased first and then decreased (SLAP2-02, SLAP2-05, SLAP2-14, SLAP2-15, SLAP2-22, and SLAP2-26). After 8 h of low temperature treatment, the expression levels of 10 SLAP2/ERF genes were all high. Under the treatment of two hormones, the expression of most genes was very low

(except that slap2-14, slap2-15 and slap2-26 were highly expressed at 12 h). Under PEG stress, the expression of some genes was significantly higher than that of the control group after 2 h. These results indicate that the SLAP2 genes could have a complex regulatory pattern in plants' resistance to abiotic stress.

Discussion

There are various kinds of environmental stresses in nature, such as biotic stress and abiotic stress; abiotic stress includes cold injury, salt injury, drought injury and flood injury. In order to resist these adverse abiotic environmental conditions, plants have developed various defense mechanisms at the molecular and physiological levels during their evolution (Cheong, 2003). There has been reported on abiotic stress in plants. On the molecular level, there are a large number of transcription factors in plants, which can respond to abiotic stresses and play a key role in regulating downstream targets. At the same time, it is quite important in plant growth, development, and response to various stresses (Mizoi et al., 2012). With the gradual publication of the whole genome of some species, the identification and

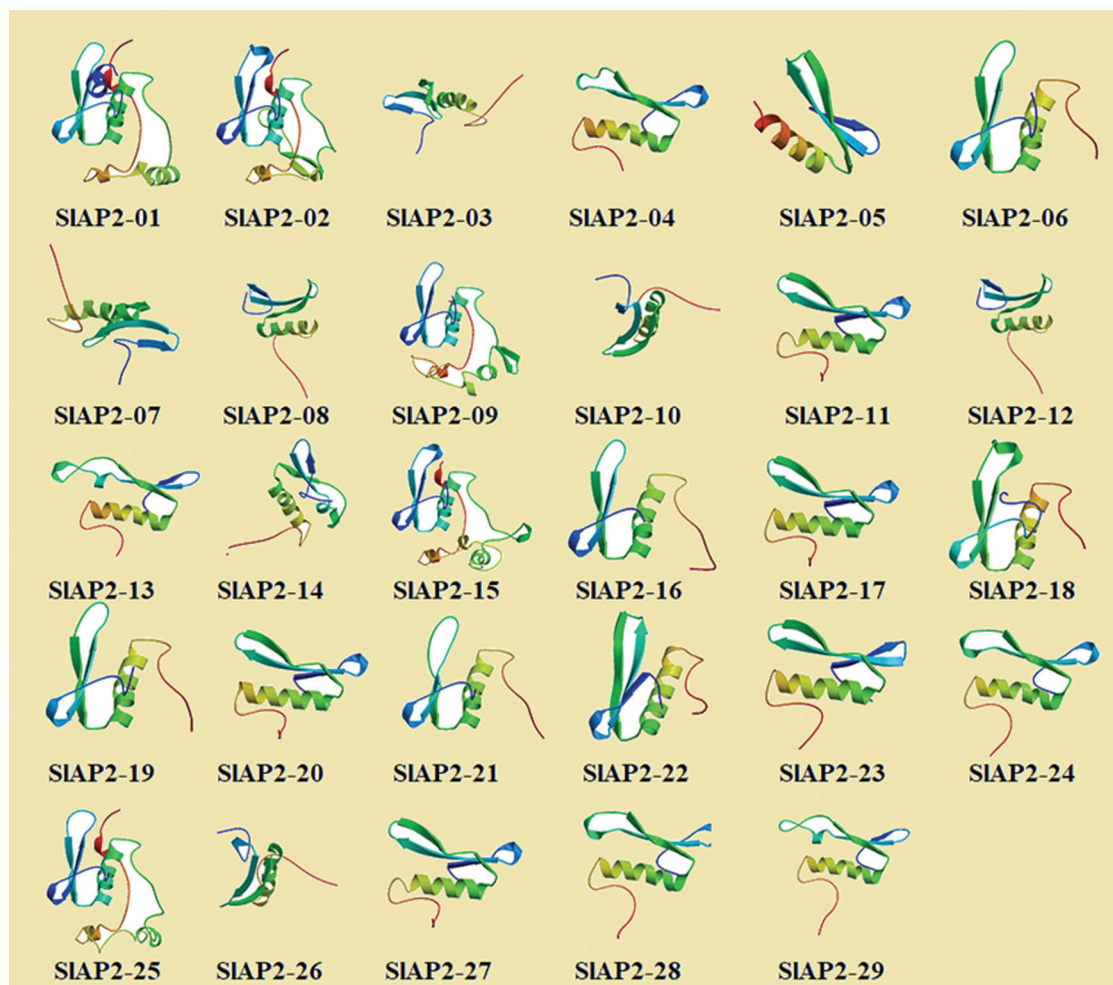


FIGURE 6. Predicted 3D models of tomato AP2/ERF proteins.

These models were constructed by the Swiss model server. Among them, template 2gcc.1.A were used in SIAP2-05; template 1gcc.1.c was used in SIAP2-23; and template 3gcc.1.A were used in SIAP2-17, SIAP2-20, SIAP2-22 and SIAP2-27; the rest of the members of SIAP2 were modelled with template 5wx91.A.

study of the classification, evolutionary characteristics, and functional prediction of gene families at the whole genome level have become the focus of genomics research. Genome-wide analysis of gene family is an effective method to describe the function of plant genes, which are helpful to study the evolution of genes and genomes. Many studies have been carried out on AP2/ERF transcription factors family and their functions in model plant *Arabidopsis thaliana*, and it has been found that AP2/ERF transcription factors family is mainly involved in plant growth and development, biotic and abiotic stress. While AP2/ERF transcription factors are widely distributed in plants, and because they can specifically bind to the cis-regulatory element in the promoter region to regulate the expression of downstream stress response genes, therefore, their role in plants under environmental stress is of great concern to researchers. AP2/ERF transcription factors have been studied in many plants, such as *Arabidopsis thaliana* (Guo *et al.*, 2005; Wang *et al.*, 2008), chickpea (Shukla *et al.*, 2006), rice (Rashid *et al.*, 2012), and maize (Lata *et al.*, 2014), and their classification and function have been reported.

However, the function of AP2/ERF in tomato has not been well studied. Therefore, we identified 29 typical AP2/

ERF genes from tomato genome. AP2/ERF gene was analyzed from the aspects of basic physical and chemical properties, phylogeny, chromosome position, gene structure, protein sequence and three-level model, cis-regulatory elements, and expression level. We constructed phylogenetic trees from 87 AP2/ERF transcription factors identified in *Arabidopsis*, potato, and tomato. The results showed that 11 SIAP2/ERF, 16 StAP2/ERF, 14 AtAP2/ERF belonged to the typical AP2 subfamily, 15 SIAP2/ERF, 8 StAP2/ERF and 16 AtAP2/ERF belonged to the typical ERF subfamily, which indicated that the evolutionary mechanism of AP2/ERF transcription factors in tomato, potato and *Arabidopsis* was similar. Meanwhile, the number of AP2/ERF gene family mainly depends on the number of members of the ERF family (Shu *et al.*, 2016), which is consistent with our study.

The domains and motifs of transcription factors have an irreplaceable effect in many plant life activities, such as protein interactions, transcriptional activity, and DNA binding (Zhao *et al.*, 2019). In this study, we identified 10 conserved motifs in SIAP2/ERF. Among them, motif1 and motif2 are conserved in all identified sequences. The study of the motif may reveal the new biological function and regulation mechanism of tomato genes. It has been suggested that TFs, which shares

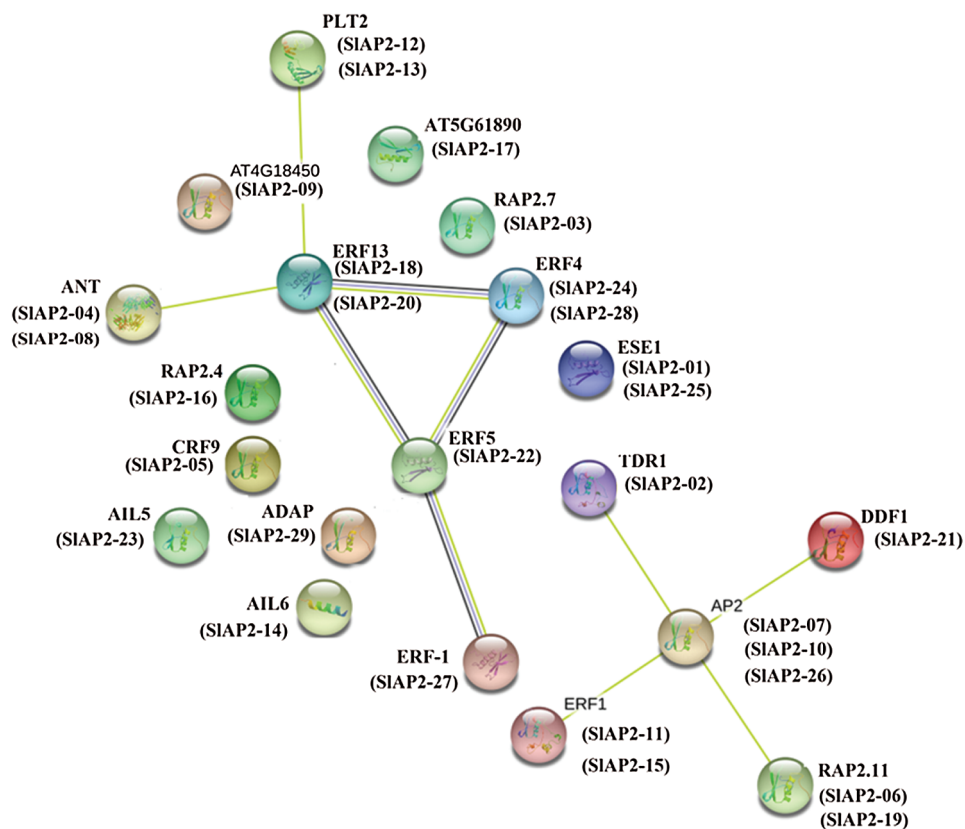


FIGURE 7. Prediction of SLAP2/ERF interaction network based on the homologous gene interaction in *Arabidopsis thaliana*.

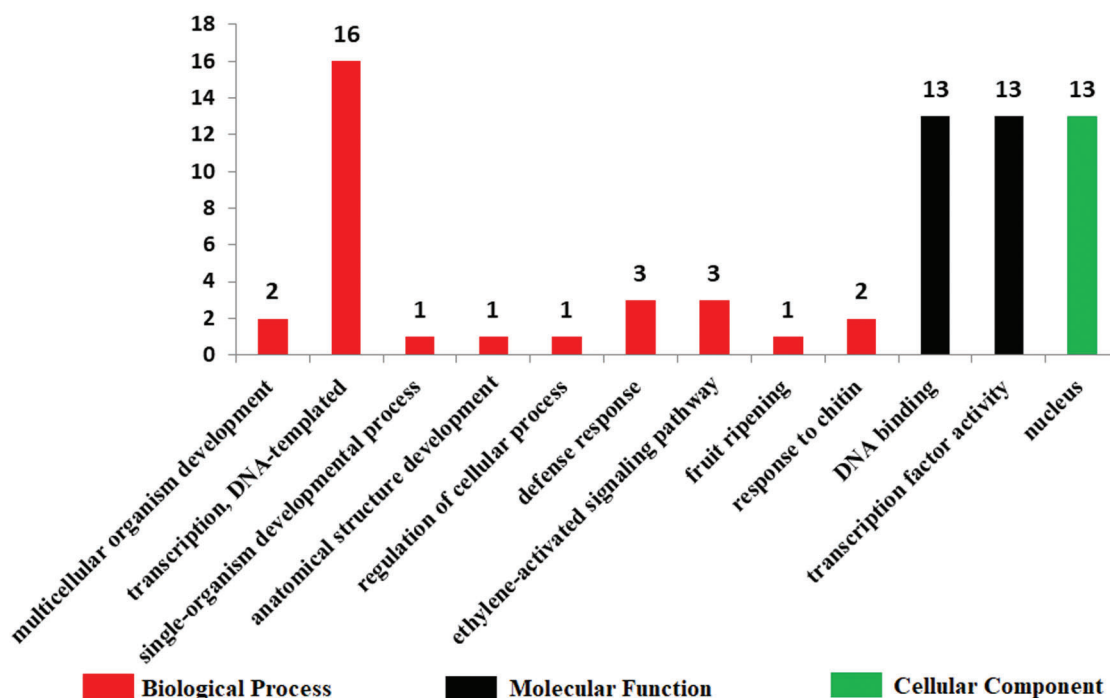


FIGURE 8. GO functional classifications of SLAP2/ERF. The result of functional classification from three levels: biological process, cellular component, and molecular function.

unique motifs in a cluster, might have similar functions. For example, in the ERF protein family, the ERF related amphiphilic suppressor (EAR) motif is specifically present in the VIII genes, which is essential for the ERF protein’s inhibitory function.

The study of gene structure can help us to further understand its function as well as the key information of evolution. In this study, we can conclude that genes of the same evolutionary branch have the same exon-intron structure. It is generally believed that genes with multiple

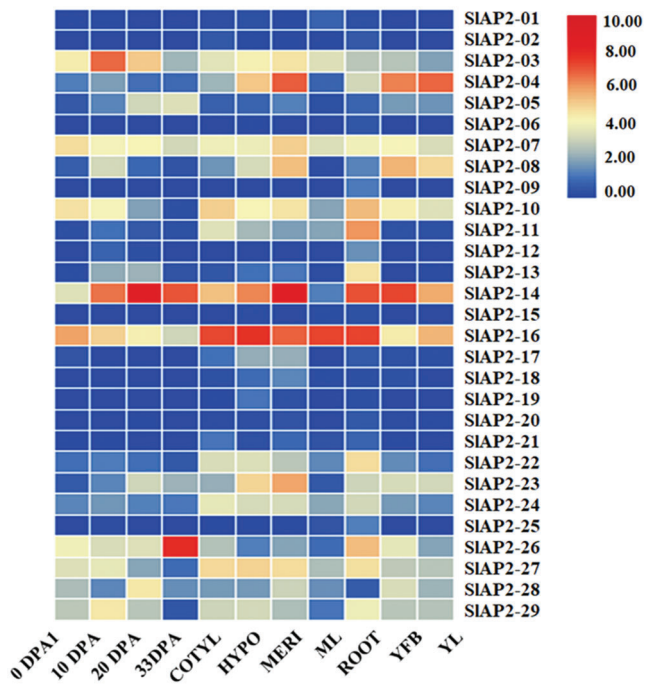


FIGURE 9. Relative expression analysis of SIAP2/ERF in different tissues.

Including flower, fruit on day 10 after flowering, fruit on day 20 after flowering, mature fruit, cotyledons, hypocotyls, meristems, mature leaves, roots, flower buds and young leaves. The $2^{-\Delta\Delta CT}$ method was used to be an evaluation of the relative expression. The heat map was drawn in row scale-transformed expression values. Red or green colors represent the difference in expression levels in each sample, respectively.

introns are conservative, while genes without introns are less conservative (Kaufmann et al., 2005). We found that 15 ERF/DREB subfamily genes and one gene (SIAP2-05) containing three AP2 domains had no intron structure, and 2 ERF/DREB subfamily members had only one intron domain, and only 3 types of conserved sequences were found in them. The number of introns in the typical 11 AP2 subfamily members is between 7 and 9. Previous studies have shown that introns gain and lose as a result of stress selection during the long-term evolution of plants, and genes gradually form various types of intron-exon structures and perform different functions (Wang et al., 2016). The results showed that the SIAP2/ERF family evolved into different subfamilies to regulate various life activities during the long-term development of the tomato genome.

Promoter, as the key DNA sequence that regulates gene expression, plays an important role in the initiation of transcription, and the number of promoters directly affects the efficiency of downstream gene transcription. The promoter region of the cis-regulatory element is irreplaceable in regulating gene expression and plant resistance to adverse environmental conditions, and the TATA-box is the key cis-regulatory element, it is essential for the correct expression of most eukaryotic genes and determines the transcription initiation site and its initiation frequency. In the present study, we identified several homeostatic components in the upstream promoter region of the SIAP2/ERF genes that respond to plant hormones,

stress and tissue-specific expression (Fig. 4). This suggests that the function of SIAP2/ERF genes is mediated by a complex regulatory network. Previous study showed that AP2/ERF protein could bind to GCC-box motif through ERF domain and regulated the expression of target gene under stress (Shigyo et al., 2006; Lata and Prasad, 2011). In this study, the homology of SIAP2-01 in *Arabidopsis thaliana*, *ESE1*, is linked to the promoter of GCC, which is involved in the regulation of gene expression. *ESE1*, as the homologous gene of SIAP2-01 in *Arabidopsis*, it is involved in the regulation of gene expression by connecting to the promoter element of GCC frame, which is related to the pathogenesis of *Arabidopsis*, and studies showed that *AtESE1* could enhance the salt tolerance (Zhang et al., 2011). So SIAP2-01 may have *ESE1*-like features. qRT-PCR results and SIAP2/ERF gene expression profiles in different tissues showed that SIAP2/ERF gene expression changed significantly under different abiotic stresses and hormone treatments. Tissue expression analysis showed that AP2/ERF genes were expressed in tomato tissues, and the expression of AP2/ERF genes was different in different tissues. Most genes are highly expressed in fruit and flowers, which is consistent with previous reports of ERF proteins involved in fruit development (Licausi et al., 2013), which may indicate that ERF genes are also involved in the development of flower organs and fruit. Abiotic stress analysis of 10 genes found that most genes were induced by stress. After 4 h of low temperature treatment, the expression of 10 genes was significantly higher than that of the control group, which is consistent with the results of previous studies on ERF participation in cold stress (Gao et al., 2014). Seven genes were significantly upregulated at 4th of salt treatment; most genes were induced by ABA and SA treatment. This provides an important basis for further studying the function and mechanism of tomato ERF transcription factor family genes. In this study, we studied potential abiotic stress response elements within 2000 bp upstream of the start codon ATG, including ABA, low temperature, drought stress, and salt stress regulatory elements. The results show that all SIAP2 genes contain these stress response elements. Based on the expression profile of qRT-PCR, we can observe SIAP2-05 and SIAP2-22 genes with two low temperature response elements (LTR), SIAP2-02, SIAP2-07, and SIAP2-26 genes containing multiple ABA response elements (ABRE), SIAP2-08, SIAP2-14 and SIAP2-26 genes with two drought response elements (MBS), SIAP2-05, SIAP2-07 and SIAP2-09 genes with several salicylic acid response elements (TCA-element), their expression levels were significantly up- or down-regulated, which was consistent with the analysis of regulatory elements and also with the results of HD-I ZIP Gene Subfamily in *Nicotiana tabacum* (Li et al., 2019). Meanwhile, these results indicated that gene expression is a complex biological process, which is regulated by many factors. Therefore, the expression mechanism of these tomato SIAP2/ERF genes needs further study.

The study of tertiary structure and protein-protein interaction can help us to understand the function of SIAP2/ERF members more clearly. The result of tertiary modeling shows that genes located in the same branch have similar tertiary structure (Fig. 5). Although the AP2/ERF gene

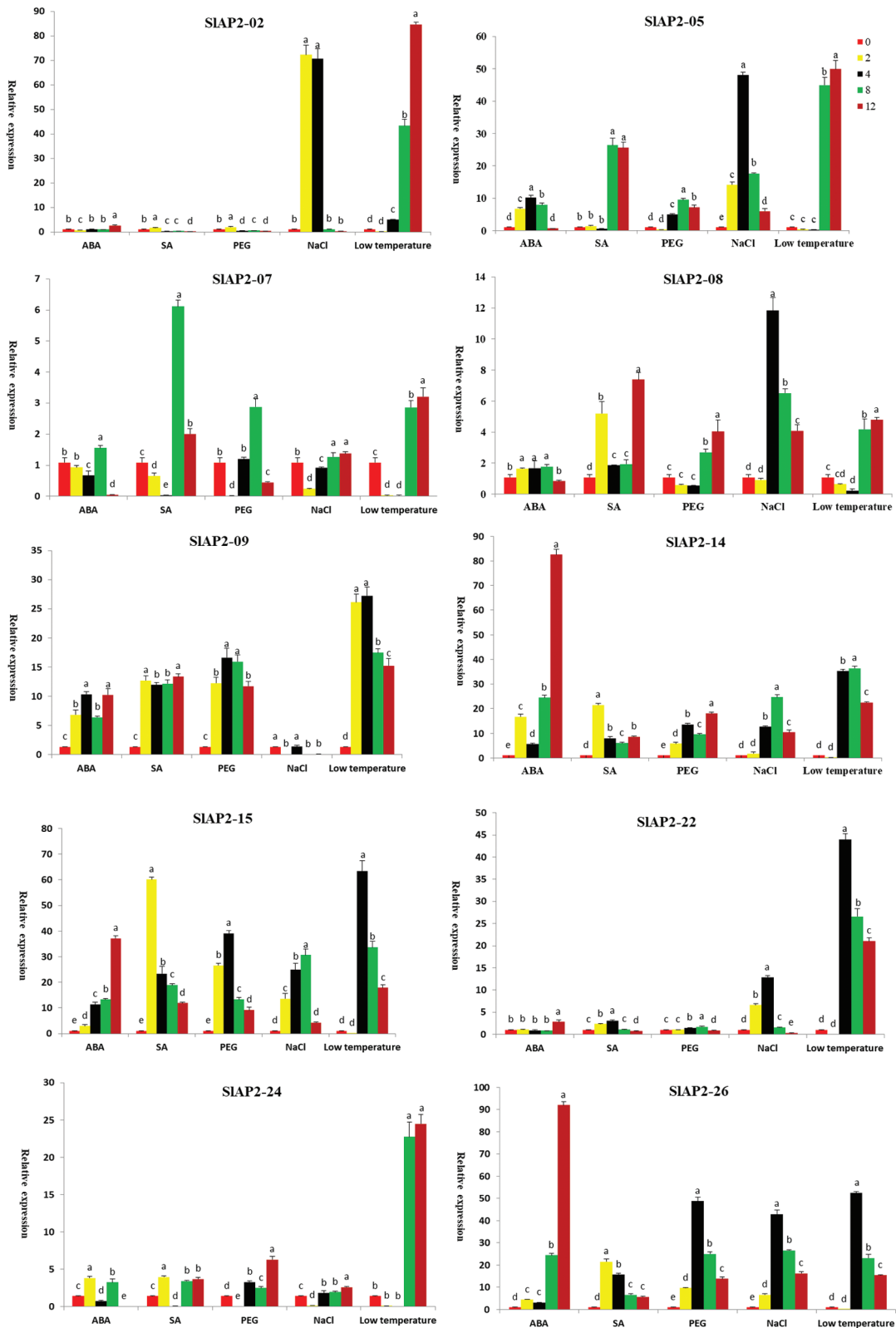


FIGURE 10. Expression patterns of 10 SLAP2/ERF under different treatments (20% PEG, 100 mmol/L NaCl, 100 umol/L ABA, 100 umol/L SA, 4°C low temperature).

Bars represent the mean values of three replicates ± standard deviation (SD). Red represents control treatment, yellow represents 2 h after processing, black represents 4 h after processing, green represents 8 h after processing, and red brown represents 12 h after processing.

family in *Arabidopsis* has been shown to influence many biological processes, relatively little has been studied in tomato, so we constructed a network of AP2/ERF protein interactions between tomato and *Arabidopsis*. Previous

results showed that *AtERF4* negatively regulated iron deficiency response in *Arabidopsis* (Liu *et al.*, 2017), and *AtERF13* endow *Arabidopsis* with ABA hypersensitivity (Lee *et al.*, 2010). Therefore, the corresponding proteins of

tomato, SLAP2-24, SLAP2-28 and AtERF4, and SLAP2-18, SLAP2-20 and *AtERF13*, have similar functions. The interaction network showed that SLAP2/ERF genes play an irreplaceable role in the development of tomato and response to abiotic and biotic stresses. Go analysis showed that SLAP2/ERF genes were widely involved in many biological processes, and were distributed in the nucleus of cells, and had DNA binding and transcription factor activity. The results showed that *CrERF5* positively regulated the biosynthesis of bisindole alkaloids and their precursors in *Catharanthus roseus* (Pan et al., 2019), and the AP2 / ERF family transcription factor GSERF71 from soybean was a DNA binding protein, which positively regulated the tolerance alkaline stress tolerance in *Arabidopsis* (Zhang et al., 2018).

Conclusion

In conclusion, we analyzed the AP2/ERF gene family of tomato at the whole genome level, and identified 29 SLAP2/ERF genes, and divided them into subfamilies. At the same time, its basic physical and chemical properties were analyzed, and the phylogenetic tree was constructed with 30 AP2/ERF proteins from *Arabidopsis thaliana* and 28 AP2/ERF proteins from potato to ensure their conservative homology. We also analyzed the chromosomal location, conserved motifs, gene structure, promoter elements, protein tertiary structure and protein interaction network of SLAP2/ERF transcription factor. Meanwhile, the expression level of SLAP2/ERF in different tissues and under different stress was detected by transcriptome and q-RT-PCR. These results provided comprehensive information for further study of the function of the SLAP2/ERF gene family.

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TABLE S1

The 87 AP2/ERF gene-coding protein sequence information in this study

Gene name	Gene Locus	Gene name	Gene Locus	Gene name	Gene Locus
SlAP2-01	Solyc09g089910.1.1	AtAP2-01	AT2G33710.1	StAP2-01	PGSC0003DMP400044184
SlAP2-02	Solyc09g066350.1.1	AtAP2-02	AT2G28550.3	StAP2-02	PGSC0003DMP400044183
SlAP2-03	Solyc10g084340.2.1	AtAP2-03	AT2G20880.1	StAP2-03	PGSC0003DMP400007140
SlAP2-04	Solyc04g077490.3.1	AtAP2-04	AT4G39780.1	StAP2-04	PGSC0003DMP400007138
SlAP2-05	Solyc04g009450.1.1	AtAP2-05	AT4G36920.2	StAP2-05	PGSC0003DMP400024338
SlAP2-06	Solyc02g067020.1.1	AtAP2-06	AT4G37750.1	StAP2-06	PGSC0003DMP400047816
SlAP2-07	Solyc02g093150.3.1	AtAP2-07	AT1G79700.1	StAP2-07	PGSC0003DMP400039351
SlAP2-08	Solyc02g092050.3.1	AtAP2-08	AT1G78080.1	StAP2-08	PGSC0003DMP400029795
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SlAP2-13	Solyc11g008560.2.1	AtAP2-13	AT1G72570.1	StAP2-13	PGSC0003DMP400048525
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Supplementary file

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 FKVSAIEKGLEVDASL'KWMGHDQNTYDGSPTLPL
 FSTAASSGFGNSANTAPSAATHQLHF
 GSGALPFP'HPSPSLTNMNLSSH'YFRS*